# THE VALUE OF OUTLINE PROCESSING IN THE BIOMETRY AND SYSTEMATICS OF FOSSILS

*by* G. H. SCOTT

ABSTRACT. Widespread use of gross dimensions and similar point-to-point measurements in biometric studies of fossils is probably due more to instrumental limitations and the influence of preceding studies than to theoretical considerations. Are such data suitable for classificatory studies which are heavily dependent on visual assessment of morphology? Theory suggests that the outlines of objects are particularly significant in visual recognition because of their high information content. They provide a parsimonious description of form. Biometry can best supplement qualitative visual processes in taxonomic studies by treating outline data in ways that replace the information lost due to the short-term, degradable nature of visual data stored in the human memory. Variation in the axial outlines of the foraminifer *Globorotalia puncticulata* (Deshayes) is examined as an example.

DATA collection is fundamental to biometry. Nevertheless, textbooks concentrate on techniques of data reduction and analysis, and offer little guidance about the collection of data. Such limited reference is understandable. Organisms are exceedingly diverse in form and organization. Guidelines for the collection of quantitative data can be cited (e.g. Simpson, Roe, and Lewontin 1960) but concepts such as 'character' and 'variable' are so context-dependent that most writers seem to concede, at least implicitly, that their selection in biometric studies should be left to the discretion of the student. While the literature indicates that there is considerable accord among researchers on protozoans to vertebrates on the types of data to be collected, this does not necessarily signify adherence to a common rationale of data collection. Precedents and instrumental constraints exert powerful influences on the data collected in a project. Here I consider the role of biometry in classificatory studies (broadly, recognition of taxa and allocation of specimens) in the light of theory on the mechanisms of visual perception. It is advocated that biometry should supplement these mechanisms by processing comparable data so that there is a parallel between qualitative and quantitative treatments of specimens. In this way biometry can contribute to resolving the problems of the systematist that arise from deficiencies in visual recognition.

## TYPICAL PRACTICE

While it is not claimed that the measurements illustrated in text-fig. 1 portray all aspects of modern practice in variate selection, they are sufficiently representative to indicate that biometric studies primarily use data on the gross dimensions of structures. Point-to-point measurements of maximum dimensions of skeletal parts form the vast majority of the data reported in the literature, and the example of the measurement of the length of a curve (text-fig. 1C) is unusual.

Instrumentation, operational convenience, and the precedents set by previous studies account for the preference for gross dimensions. The first two, in conjunction, are fundamental. Operationally, gross dimensions offer considerable advantages in variate selection. Much of the form of skeletal structures consists of smooth, continuously curved surfaces. In such regions well-defined, relocatable loci for measurement may be few, and the obvious 'landmarks' for the biometrician are the extremities of the structure. Usually these are homologous within the population sampled. The simple scales and calipers which are the stock in trade of the palaeontologist are well suited to measurements of gross dimensions, whereas they are unsuited to determining the lengths of vectors or curves, for example. Indeed, the widespread use of gross dimensions and of measurements between

[Palaeontology, Vol. 23, Part 4, 1980, pp. 757–768.]

well-defined 'landmarks' in biometry is probably due as much to the limitations of instruments as to their value on purely biological grounds in morphological description and analysis.

Precedent is an ancillary influence that tends to stabilize the set of characters measured and perhaps inhibits fresh consideration of what should be measured. Moreover, pioneering works that use point-to-point measurements have an advantage in the selection of precedents because of the general availability of comparable measurement devices. The measurements (partly shown in text-fig. 1A) on trilobites made by Shaw (1957) are a good example of the influence on later workers (Temple 1975) of a pioneering study.

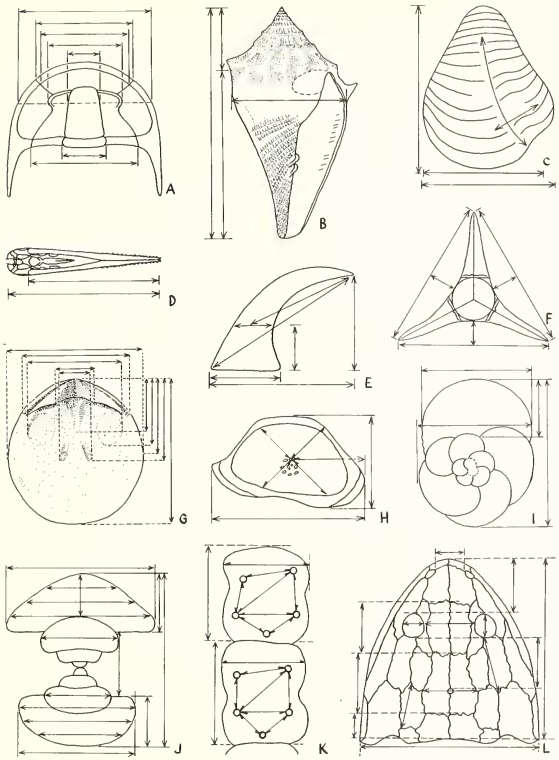
## A BASIS FOR BIOMETRY

There is very little evidence in the literature that theoretical considerations have influenced the choice of characters for measurement. In an introduction to a major biometric study of Ostracoda, Reyment (1963) asserted that statistical analysis would provide a comprehensive representation of variation but made no comment on the adequacy of the measurements (carapace length, height, and breadth) that formed the great majority of his data. It is conjectural whether the claim by Hallam and Gould (1975, p. 517) that their nine measurements on the left valve of *Gryphaea* are 'adequate to express overall features of valve shape and the character of the sulcus' can be substantiated. Most workers (myself included) can be easily pilloried on the grounds of *ad hoc* selection of data without justification. A relevant example is Melville's (1978) critique of a biometric study of leaf shape in *Ulmus*. Which features should be selected for measurement?

The choice of measurements and their analysis should relate to the aims and methods of the investigation. This is self-evident in an application of biometry to a study of functional morphology, for example, where mechanical hypotheses are presented for testing. But it is a useful point of departure when considering the role of biometry in the generally less-structured tasks of classification. Here the primary activities concern the establishment of classes and the allocation of specimens. The principal problems concern the estimation of intra-group variation and inter-group separation or distance. Where do class limits fall? Modern evolutionary theory and research provide a cogent account of the mechanisms of variation. The systematist, however, is presented with the end products of various genetic, phenotypic, ontogenetic, and diagenetic processes. In a particular instance there may be very strong reasons, *a priori*, to suppose that the specimens under systematic scrutiny are samples from discrete populations. The problem is that of recognition.

Although data on distribution and ecology are significant, the primary information in the systematics of fossils is morphological, obtained by qualitative visual examination. The immense production of illustrations of fossils over the last two centuries attests the fundamental importance of visual representation in systematics. Certainly, the initial phase of simple qualitative visual assessment is followed by analysis, sometimes using quantitative data, that leads to diagnoses of taxa. But the latter is a conscious refinement of the initial phase. The brain is an immensely fast and powerful processor of visual imagery. Visual data are rapidly assembled, images reconstructed and interpreted. Messages about the identity of specimens are produced almost involuntarily and are the basis of classificatory work. The process is that used in other visual recognition tasks in day-to-day experience, although a higher standard of recognition and discrimination is desirable. Form variation in biological materials is often complex, with major ontogenetic and environmental sources to be allowed for in taxonomic recognition.

What is the role of biometry in such studies? Should it supplant or supplement qualitative perception? If only for reasons of instrumentation, the present role must be supplementary. In many aspects the human visual system is more advanced than any similar device. It is in inter-image discrimination that the human system is least effective, especially when sample sizes are large, variation multidimensional, and groups ill defined. Objects are scanned and features of others recalled in attempts to reach classificatory decisions. Here the static, long-term memories of digital devices seem to have marked advantages over the human system. Re-recording of image information to refresh the memory is made unnecessary. Once stored, it remains available for recall and



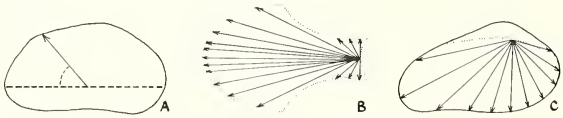

TEXT-FIG. 1. Measurements of structures commonly preserved as fossils. Variate identifications and scales are omitted in the adaptations. A, non-agnostidean trilobite cephalon after Shaw (1957, text-fig. 11). B, gastropod, *Athleta petrosa* (Conrad), after Fisher, Rodda, and Dietrich (1964, text-fig. 1). C, bivalve, *Gryphaea*, after Hallam and Gould (1975, fig. 1). D, pterosaur skull, *Pterodactylus*, after Mateer (1976, fig. 1). E, conodont, after Sergeyeva *et al.* (1975, fig. 5). F, acritarch, after Sellberg and Kjellstrom (1975, fig. 1). G, brachiopod, *Linnarssonella girtyi* Walcott, after Rowell (1966, table 4). H, ostracod, *Bairdia victrix* Brady, after Cadot and Kaesler (1973, fig. 2). I, foraminifer, *Globorotalia miozea miozea* Finlay, after Scott (1972, text-fig. 2). J, ammonite, *Vascoceras*, after Berthou, Brower, and Reyment (1975, fig. c). K, molar teeth of condylarth mammal, after Olson and Miller (1958, fig. 61). L, amphibian skull, *Trimerorhachis*, after Olson (1953, fig. 1).

reprocessing without degradation. If biometry is to supplement the 'weak' points of visual perception, it follows that it should process the same sort of data. The problem with *ad hoc* characters is that they may record aspects of the object that are insignificant in visual processing. How does the human system function?

*Visual perception*. Once the preserve of the psychologist, the mechanics of visual perception have become an interdisciplinary subject because of their relevance in automatic pattern recognition and allied studies. A comprehensive survey is not attempted, but there is general agreement about the significance of the outline in object recognition. Gestalt psychologists (e.g. Koffka 1935) concentrated on those properties of figures that facilitated their recognition or isolation from background data. One of their laws of organization drew attention to the importance of closure. Closed figures tend to be perceived as units more readily than unclosed. From quite different premises, information theorists showed that much visual data is redundant in recognition processes because of high correlation among the data received by adjacent visual receptors. Attneave (1954) gave a simple, convincing, example of this and suggested that early visual processing filters out much redundant information, leaving a reduced, more economic, description of the data. Redundancy is high in regions of an object that are homogeneous in some visual property (e.g. colour, texture, curvature) and low in regions where such properties change rapidly. The margins of an object are regions where redundancy is particularly low, although zones of uniform slope or curvature along the margin have higher redundancy than those in which there are rapid changes in direction or slope. Attneave showed that an object can be recognized readily from a simplified sketch consisting of the points of maximum curvature of the outline linked by straight lines. Such a result is an explanation of the verisimilitude achieved so effortlessly by the competent cartoonist or street artist. But it is also highly suggestive to the biometrician. Marr (1976) suggested that a major element in early visual processing is the construction of a 'primal sketch' from grey-level changes in the receptor data array. Intensity changes are isolated and used to construct a description of the array. Edges are major elements in the description.

*Commentary*. The review indicates the prime importance of outline data in visual recognition. There will be many examples in which data, highly significant for recognition, lie within the outline. But, in general, treatment of the outline is a suitable commencement for biometry in classificatory studies. Measurement loci, as shown in text-fig. 1, show various degrees of compatibility with Attneave's interpretation of visual perception. Some are located on outline segments of low curvature to which the eye gives little attention (e.g. text-fig. 1H, I). Others (e.g. text-fig. 1F) are on outline segments of high curvature that are probably significant in object recognition. However, the use made of measurement loci in most biometrical practice differs considerably from that suggested by the foregoing theory. Biometricians have recorded distances between loci, whereas theory suggests that it is the position of loci as well as interloci distances that is important in perception. A vectorial approach is indicated.

Vectorial data have been collected in previous studies (text-fig. 2), although not as implementations of the rationale developed above. Examples are Anstey and Delmet (1973) and Cheetham and Lorenz (1976) on bryozoans, Christopher and Waters (1974) on miospores, Gevirtz (1976) and Pastiels (1953) on bivalves, Kaesler and Waters (1972) and Margerie (1977) on ostracods, Scott




TEXT-FIG. 2. Examples of outline recording. A, ostracod, *Eucypris*, after Margerie (1971, fig. d). B, cheilostome bryozoan, after Cheetham and Lorenz (1976, fig. 4). C, bivalve, *Carbonicola*, after Pastiels (1953, fig. 4).

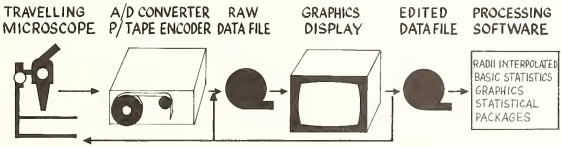
(1976) on foraminifera, and Waters (1977) on blastoids. A common aim has been to describe accurately the form of the specimen outline. Although representative outlines were presented in several studies, data have not usually been presented in ways that assist in the resolution of taxonomic problems. For example, assemblies of outlines (pictograms) have, in the light of the previous discussion, good theoretical support as effective presentations of intra-sample variation. The problem of specimen organization within the pictogram can be readily resolved if outline coordinates are available.

## TECHNIQUE AND AN EXAMPLE

This section gives some simple representations of outline data that are useful in classificatory studies.

*Data capture.* Text-fig. 3 summarizes the data logging and processing system. The digitizer attached to the stereomicroscope (Scott 1975) was built to specification and is suitable for fossils with greatest diameters between 0·05 mm and 40 mm. It is manually guided (by movement of the travelling head) and the $x$, $y$ coordinates of loci selected by the operator are recorded in units of 5·3 $\mu$m on paper tape.

Specimens are digitized in a standard orientation. Errors in orientation are minimized when specimens have two or more structures that are small in relation to the accuracy of the measurement system and occur in invariant positions. Such structures are seldom available. In the example, the axial profiles of the shell were recorded with the coiling axis aligned east–west with reference to a cross-line in the ocular lens. The coiling axis in foraminifera and similar shells is not a physical structure, but its position can be estimated from the location of the proloculus (initial chamber) and umbilicus.

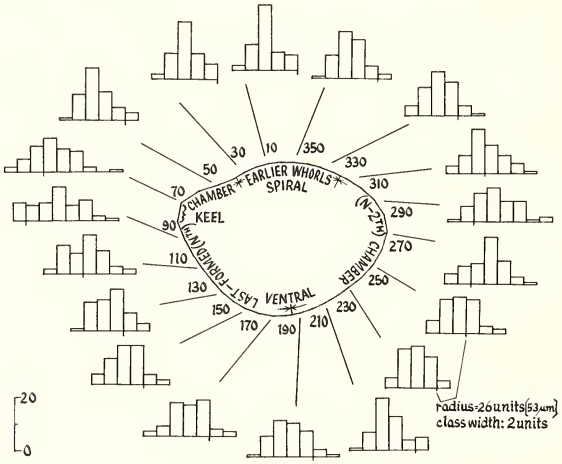



TEXT-FIG. 3. Flow diagram of data capture, editing, and processing system. The equipment includes a custom-built digitizer, Tektronix 4006 graphics display, Hewlett Packard 7202A graphics plotter, and Hewlett Packard 2100, Burroughs B6700, and IBM 370/168 processors.

*Editing.* Errors due to mis-positioning (backlash, parallax, involuntary movement) increase in importance as the size of the specimen or structure decreases. Graphical editing of the recorded $x$, $y$ data is highly desirable. With batch processing much can be done using lineprinter plots and editing runs, but interactive editing with a graphics terminal is preferable. My equipment displays $x$, $y$ coordinates in order of recording and joined by straight lines (the specimen is represented as a polygon). Coordinates may be inserted or deleted and the figure redisplayed.

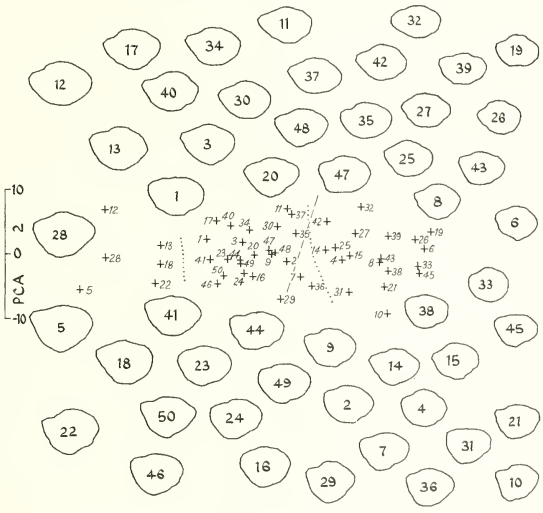
*Reconstruction.* I record about fifty loci approximately equidistant about the periphery of the specimen. There is no quantitative control over their position relative to the starting-point. Thus the *ith* point on one specimen is not necessarily positionally equivalent to the *ith* point on another. Another consideration is that only the obviously spurious coordinates can be removed by editing. A residual of small-scale errors in positioning remains in the data. Smoothing of the data and interpolation of points at fixed positions about the periphery are performed by fitting a Fourier Series curve to each specimen. An angular expansion of the radius about the specimen centroid is applied (Ehrlich and Weinberg 1970). Radii are interpolated at 10° intervals using 15 harmonics. This produces mild smoothing. Note that this expansion is suitable only for generally convex figures in which radii are single-valued. All subsequent processing uses the file of interpolated radii.

*Variation in* Globorotalia puncticulata sphericomiozea. Referred to this upper Miocene-lower Pliocene planktonic foraminiferal taxon are New Zealand populations that are intermediate in morphology and stratigraphic position between *Globorotalia miozea conoidea* Walters and *G. puncticulata puncticulata* (Deshayes). In axial orientation *G. miozea conoidea* is weakly conical with the base formed by the flattish spiral of the early whorls and the cone by the ventrally extended chambers of the last whorl (for terminology see text-fig. 4). The keel at the shell margin is well defined on the last-formed chamber but is usually buried by secondary calcification on earlier chambers. The form of the shell in *G. puncticulata puncticulata* is globose, rather than conical. This is produced by moderate inflation of chambers. Straight-line segments of the chamber outline are replaced by gentle curves. There is no keel. At some horizons, some specimens of *G. puncticulata sphericomiozea* have the axial form of the ancestral *G. miozea conoidea* (and its variant *G. conomiozea* Kennett). Others anticipate the shape of *G. puncticulata puncticulata*. Blow (1969 p. 361) suggested that such samples represented a mixture of two taxa on the hypothesis that keels, once evolved, are thereafter retained in phylogeny. He rejected the idea of populations in which some specimens possessed a keel and others did not. Although there is no theoretical support for the permanency of a structure, Blow's suggestion about mixed samples warrants study because Kennett (1977) showed that there was marked deterioration in climate in the New Zealand region in the uppermost Miocene, about the stratigraphic position of *G. puncticulata sphericomiozea*. Changes in the distribution of planktonic taxa in response to shifts in watermasses and the appearance of migrants are to be expected in such a regime. To assess Blow's idea, the systematist needs to examine intra-sample variation. Is it continuous? Can sub-sample clusters be detected? Here, the axial outline of the shell is examined. This profile provides information on the shape of chambers near the location of the keel at the shell periphery. The topics considered are the construction of a typical outline, and the pictorial representation of within-sample variation.




TEXT-FIG. 4. Histograms show distributions of radii at 20° intervals about centroids of fifty specimens of *Globorotalia puncticulata sphericomiozea* Walters from P29/f55, Blind River, New Zealand. The polygonal outline is formed from the mean lengths of radii spaced at 10° intervals.

*Outline representations.* The distributions of radii (text-fig. 4) about the centroid of the axial outline of fifty specimens from P29/f55 Blind River (close to sample 32 in Kennett and Watkins 1974), show some variation in kurtosis but tend to be unimodal. The outline in the centre of text-fig. 4 is drawn from mean values of the thirty-six radii and reflects common features in the sample outlines shown in text-fig. 5. Gentle doming in the vicinity of the spire, rapid change in curvature of the outline of the *n*th chamber at the site of the keel, and ventral extension of chambers are features of most of the outlines in text-fig. 5 that are also apparent in the sample mean outline.

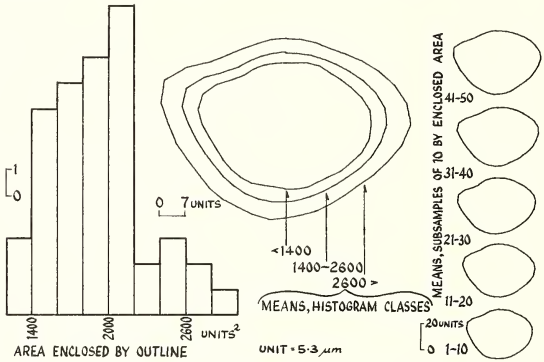



TEXT-FIG. 5. Plot of sample from P29/f55 (fifty individuals) on two largest principal component axes (dispersion matrix, thirty-six radii as deviations from means). PCA 1 and PCA 2 represent 81% and 6% of sample variance. Location of axial outlines of specimens is related to their position in the plot (objectively defined pictogram). Dotted lines show three-cluster division of sample using the non-hierarchical clustering algorithm (sum of squares criterion) in GENSTAT (statistical package produced by Rothamsted Experimental Station) and dashed line is the two-cluster partition. This algorithm transfers specimens between clusters to improve the criterion but a global optimum is not necessarily reached.

However, use of the sample mean outline as a representative form in comparisons among taxa is contingent on negligible shape change within the sample size range. If allometry is marked, the sample mean outline may be quite unrepresentative, not corresponding with the shape of any specimen. Size-related changes in shape complicate taxonomic recognition and may require special study. Brower and Veinus (1978) discussed an approach suitable for vectorial data. In the example, mean outlines for five size-defined subsamples (text-fig. 6) are similar, and even specimens from the extreme size classes show close resemblance, although there is a modest radial extension of the outline

in the vicinity of the ($n$–2)th chamber of the largest specimens (text-fig. 6 centre). I conclude that size-related shape changes within the material do not greatly affect the use of the sample mean outline as a representative form.

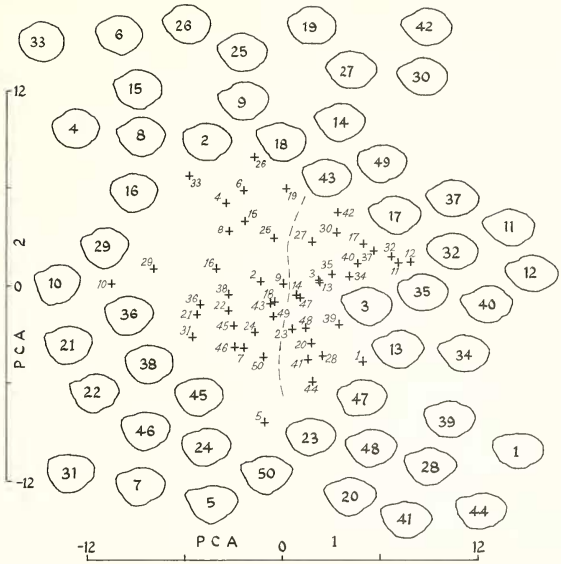
There is a minority of specimens (e.g. 16, 23, 33 in text-fig. 5) in which spiral and ventral segments of the outline of the $n$th chamber form a rounded rather than an angular junction (70–90° radii in text-fig. 4). In this respect they resemble *G. puncticulata puncticulata*. Do they form an identifiable subsample? A quantitative or metric version of the pictogram (text-fig. 5), in which outlines are referred to specimen positions on a principal component plot, shows that such specimens are scattered through the sample. Thus specimens 12 and 45 lie at opposite ends of the distribution along PCA 1 which represents much of the intra-sample variation in outline size. PCA 2 reflects variation in the degree of ventral inflation of the outline. Again, there are specimens (e.g. 12, 16) that show considerable difference in ventral inflation yet have rounded peripheries.




TEXT-FIG. 6. Histogram shows distribution of area enclosed by outlines (axial profile) of fifty specimens from P29/f55. Area is taken as a natural measure of size. The superimposed outlines used subsamples based on the histogram intervals. Outlines at right were formed by ranking the fifty specimens by area and dividing them into five equal subsamples.

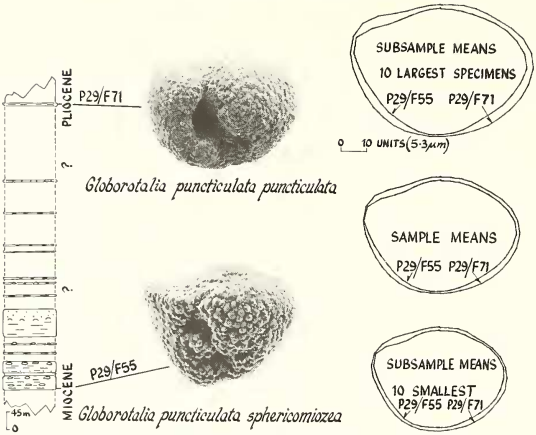
If size can be neglected in a taxonomic judgement it is useful to examine a representation in which it is held constant (text-fig. 7). Much of the arrangement of text-fig. 5 is preserved but there are several displacements that clarify shape similarities. For example, specimen 1 (low spire, weak axial inflation) lies on the periphery of the scatter in text-fig. 7 whereas in text-fig. 5 it lies between specimens 3 and 13. Specimens 33 and 45 are dissimilar in shape but their common size causes their close proximity in text-fig. 5. They are widely separated in text-fig. 7. A group of specimens with weak axial inflation and a slight dome representing the early chambers (e.g. specimens 11, 12, 17, 32, 37, 40) are in closer proximity in text-fig. 7 than in text-fig. 5.

Distinct clusters are not obvious in text-figs. 5 and 7. This impression is supported by the intra-sample divisions produced by a non-hierarchical clustering algorithm in GENSTAT. Large specimens are isolated by the procedure using raw data (text-fig. 5, 3-cluster partition) but 2-cluster partitions using either raw or size-standardized data separate specimens that are similar in shape and in close proximity in the principal component plots. The partitions are placed in a central location in the scatter. This results from the fairly uniform distribution of specimens in the hyperspace.




TEXT-FIG. 7. Principal component plot of the sample from P29/f55 using thirty-six radii (as deviations from means) after areas of outlines were standardized. Radii were incremented/decremented iteratively until the area of each polygonal outline fell within 5% of an arbitrary constant, close to the mean of the enclosed area distribution using raw data. Axes PCA 1 and PCA 2 represent 30% and 24% of sample variance (dispersion matrix). The dashed line is the location of the two-cluster partition produced by the non-hierarchical clustering algorithm in GENSTAT (sum of squares criterion). Axial outlines of specimens using standardized data are arranged according to their locations in the plot.

The data in text-figs. 4–7 indicate that a variable population was sampled, even when size is eliminated. But the representations show gradations in form and the absence of well-defined disjunctions in specimen distributions. A connection is not observed between the form of the periphery of the *n*th chamber and the gross axial shape of the shell. These results assist the taxonomist to assess the validity of *G. puncticulata sphericomiozea* in the light of Blow's hypothesis. Inter-sample comparisons may also be useful. Text-fig. 8, for example, indicates the changes in axial form between *G. puncticulata sphericomiozea* and *G. puncticulata puncticulata* much more explicitly than do direct comparisons of specimen suites. In the latter the outline of the *n*th chamber about the 30–70° segment (see text-fig. 4 for locations) is raised relative to the equivalent segment in *G. puncticulata sphericomiozea*. This occurs throughout the size range sampled. But in the 110–150° segment of the *n*th chamber, inflation relative to *G. puncticulata sphericomiozea* is marked only in larger specimens. The study of the transformation in shape between the taxa leads to techniques reviewed by Bookstein (1977).




TEXT-FIG. 8. Inter-sample comparisons of outlines. Location of samples P29/f55 and P29/f71 in the Blind River sequence, scanning electron micrographs of random specimens of *Globorotalia puncticulata puncticulata* (Deshayes) and *G. puncticulata sphericomiozea* Walters, and superimposed outlines from the samples.

## CONCLUSION

I do not contend that biometric studies using *ad hoc* variates should be abandoned. Rather, I suggest that analyses with these variates usually do not integrate easily with qualitative assessment of form. Generally, they provide an inadequate representation of the outline and may include measurement loci not significant in visual recognition. Vector relationships between measurements are entirely omitted yet are essential in object identification. By processing the coordinates of outlines, a quantitative study provides information that is easily and directly related to the material posing a classificatory problem, and amenable to statistical testing. Of course, outline data may also contain significant functional information. For example, the form of the shell of an infaunal burrower is likely to show adaptations to the mechanism of movement.

Representation of outlines by polar coordinates requires large sets of data that may cause housekeeping problems on small computers. There is commonly some redundancy in the variate set (dispersion matrices less than full rank) and a more parsimonious set is possible. However, the set provides directly a polygonal representation of form which is easy to manipulate (magnification, rotation, reflection) and from which image descriptors (Rink 1976) and *ad hoc* variates can be derived readily. The verbal descriptors of Riedel (1978) are less exact and less suitable for simple graphical reconstructions and manipulations. The techniques of numerical taxonomy and automated identification (Sneath 1979) usually operate with character states, selected by the investigator, and do not provide shape representations at the basic population level.

Outlines are rich in information for the taxonomist. That is why they should be used in biometry. Nevertheless, they are only a point of departure. Systems that process all pictorial information from a specimen suite in various orientations offer the prospect of much more sophisticated assistance to the taxonomist.

*Acknowledgements*. I am grateful to A. H. Cheetham, B. W. Hayward, and N. de B. Hornibrook for reviewing a draft of this paper.

## REFERENCES

ANSTEY, R. L. and DELMET, D. A. 1973. Fourier analysis of zooecial shapes in fossil tubular bryozoans. *Bull. geol. Soc. Am.* **84,** 1753–1764.

ATTNEAVE, F. 1954. Some informational aspects of visual perception. *Psychol. Rev.* **61,** 183–193.

BERTHOU, P. Y., BROWER, J. C. and REYMENT, R. A. 1975. Morphometrical study of Choffat's vascoceratids from Portugal. *Bull. geol. Instn Univ. Uppsala* N.S. **6,** 73–83.

BLOW, W. H. 1969. Late middle Eocene to Recent planktonic foraminiferal biostratigraphy. *In* BRÖNNIMANN, P. and RENZ, H. H. (eds.). *Proceedings of the First International Conference on Planktonic Microfossils*, Brill, Leiden, 1, 199–421.

BOOKSTEIN, F. L. 1977. The study of shape transformation after D'Arcy Thompson. *Math. Biosci.* **34,** 177–219.

BROWER, J. C. and VEINUS, J. 1978. Multivariate analysis of allometry using point coordinates. *J. Paleont.* **52,** 1037–1053.

CADOT, H. M. and KAESLER, R. L. 1973. Variation of carapace morphology of bairdiacean and cytheracean Ostracoda. *Paleont. Contr. Univ. Kans.* **61,** 1–10.

CHEETHAM, A. H. and LORENZ, D. M. 1976. A vector approach to size and shape comparisons among zooids in cheilostome bryozoans. *Smithson. Contr. Paleobiol.* **29,** 1–55.

CHRISTOPHER, R. A. and WATERS, J. A. 1974. Fourier series as a quantitative descriptor of miospore shape. *J. Paleont.* **48,** 697–709.

EHRLICH, R. and WEINBERG, B. 1970. An exact method for characterization of grain shape. *J. sedim. Petrol.* **40,** 205–212.

FISHER, W. L., RODDA, P. U. and DIETRICH, J. W. 1964. Evolution of the *Athleta petrosa* stock (Eocene, Gastropoda) of Texas. *Univ. Tex. Publs* **6413,** 1–117.

GEVIRTZ, J. L. 1976. Fourier analysis of bivalve outlines: implications on evolution and autecology. *J. Int. Ass. Math. Geol.* **8,** 151–163.

HALLAM, A. and GOULD, S. J. 1975. The evolution of British and American middle and upper Jurassic *Gryphaea*: a biometric study. *Proc. R. Soc. Lond.* **B 189,** 511–542.

KAESLER, R. L. and WATERS, J. A. 1972. Fourier analysis of the ostracod margin. *Bull. geol. Soc. Am.* **83,** 1169–1178.

KENNETT, J. P. 1977. Cenozoic evolution of Antarctic glaciation, the circum-Antarctic Ocean, and their impact on global paleoceanography. *J. geophys. Res.* **82,** 3843–3860.

—— and WATKINS, N. D. 1974. Late Miocene-early Pliocene paleomagnetic stratigraphy, paleoclimatology, and biostratigraphy in New Zealand. *Bull. geol. Soc. Am.* **85,** 1385–1398.

KOFFKA, K. 1935. *Principles of gestalt psychology*. Routledge & Kegan Paul, London, 720 pp.

MARGERIE, P. 1971. Essai de 'quantification' du contour des ostracodes a l'occasion de la description d'une nouvelle espèce de Cypridinae du Marinésien du bassin de Paris. *Revue Micropaléont.* **14,** 227–234.

—— 1977. Complément a deux articles antérieurs (1969–1972) relatifs a l'utilisation de la statistique pour la description des ostracodes. Ibid. **20,** 44–48.

MARR, D. 1976. Early processing of visual information. *Phil. Trans. R. Soc. Lond.* **B 275,** 483–524.

MATEER, N. J. 1976. A statistical study of the genus *Pterodactylus*. *Bull. geol. Instn. Univ. Uppsala*, N.S. **6,** 97–105.

MELVILLE, R. 1978. On the discrimination of species in hybrid swarms with special reference to *Ulmus* and the nomenclature of *U. minor* Mill. and *U. carpinifolia* Gled. *Taxon*, **27,** 345–351.

OLSON, E. C. 1953. Integrating factors in amphibian skulls. *J. Geol.* **61,** 557–568.

—— and MILLER, R. L. 1958. *Morphological Integration*, Univ. Chicago Press, Chicago, 317 pp.

PASTIELS, A. 1953. Étude biometrique des Anthracosiidae du Westphalien A de la Belgique. *Publs Ass. Etude Paléont. Stratigr. houill.* **16,** 1–56.

REYMENT, R. A. 1963. Notes on the description of post-Paleozoic fossil ostracods. *J. Paleont.* **37,** 682–687.

RIEDEL, W. R. 1978. Systems of morphologic descriptors in paleontology. Ibid. **52,** 1–7.

RINK, M. 1976. A computerized quantitative image analysis procedure for investigating features and an adapted image process. *J. Microsc.* **107,** 267–286.

ROWELL, A. J. 1966. Revision of some Cambrian and Ordovician inarticulate brachiopods. *Paleont. Contr. Univ. Kans.* **7,** 1–36.

SCOTT, G. H. 1972. The relationship between the Miocene Foraminiferida *Globorotalia miozea miozea* and *G. praemenardii*. *Micropaleontology*, **18,** 81–93.

SCOTT, G. H. 1975. An automated coordinate recorder for biometry. *Lethaia*, **8**, 49–52.

—— 1976. Estimation of ancestry in planktonic foraminifera: *Globoquadrina dehiscens*. *N.Z. J. Geol. Geophys.* **19**, 311–325.

SELLBERG, B. and KJELLSTROM, G. 1975. Geometric characterization of acritarchs belonging to the genus *Veryhachium*. *Neues Jb. Geol. Palaont.*, Mh. **1975**, 310–314.

SERGEYEVA, S. P. 1975. Orientation, morphological terminology and measurements of simple conodonts. *Paleont. J.* **9**, 385–391.

SHAW, A. B. 1957. Quantitative trilobite studies II. Measurement of the dorsal shell of non-agnostidean trilobites. *J. Paleont.* **31**, 193–207.

SIMPSON, G. G., ROE, A. and LEWONTIN, R. C. 1960. *Quantitative Zoology*, Harcourt Brace, New York, 440 pp.

SNEATH, P. H. A. 1979. Numerical taxonomy and automated identification: some implications for Geology. *Computers and Geosciences*, **5**, 41–46.

TEMPLE, J. T. 1975. Standardization of trilobite orientation and measurement. *Fossils and Strata*, **4**, 461–467.

WATERS, J. A. 1977. Quantification of shape by use of Fourier analysis: the Mississippian blastoid genus *Pentremites*. *Paleobiology*, **3**, 288–299.

G. H. SCOTT

N.Z. Geological Survey
P.O. Box 30368
Lower Hutt
New Zealand

Typescript received 13 September 1979
Revised typescript received 26 November 1979